

## Prey-predator dynamics driven by the solar radiation - Part I

L. SERTORIO and G. TINETTI

*Dipartimento di Fisica Teorica, Università di Torino - Torino, Italy*  
*Istituto Nazionale di Fisica Nucleare, Sezione di Torino - Torino, Italy*

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**Summary.** — We study a model ecosystem represented by two components: prey and predator. The predator feeds only on the prey, the prey, in turn, feeds on the solar radiation. In this scheme the two-species dynamics is no longer independent of the external physical conditions. Such independence was instead postulated in the Lotka-Volterra scheme. In this paper we consider the growth of the prey not unbounded (exponential), but logistic, where the saturation factor is governed by the available solar flux, more precisely by the percent of the solar flux that contains the photon frequencies which can drive the photosynthesis. In this way the solar flux represents the driving term of the dynamics, as we expect in general for a realistic ecosystem. The system is asymptotically stable. The equilibrium values of the prey and predator numbers depend on several parameters. The system contains two nonlinear coupling terms and two coupling parameters. The dependence of the equilibrium point on the coupling parameters is studied in detail. According to this model, we can define a predator efficiency and a global solar efficiency. We discuss the relationship between these two functions of the coupling parameters and the maximum value that the predator population can reach.

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### 1. – The Lotka-Volterra system

In this section we present some concepts and known results that help in the understanding of the new model that will be developed in the following sections.

The Lotka-Volterra system belongs to the type of equations describing collective behaviours. By collective behaviour we mean that a “population”  $n(t)$  (atoms, members of a species, the amount of a reservoir) changes in time in such a way that each member, or parcel of such population, behaves exactly as any other one. More precisely we have

1) Collective growth or decay:

$$(1.1) \quad \frac{dn}{dt} = \pm an(t), \quad n(t=0) = n_0,$$

with solution

$$(1.2) \quad n(t) = n_0 e^{\pm at}.$$

2) Collective growth with saturation:

$$(1.3) \quad \frac{dn}{dt} = an(t)(n^{\max} - n(t)), \quad n(t=0) = n_0.$$

Equation (1.3) says that  $n(t)$  changes in proportion to the joint effect of  $n(t)$  itself and the “residual”  $n_{\max} - n(t)$ ; this residual is the saturation factor. Equation (1.3) is sometimes called Verhulst equation. Its solution is known:

$$(1.4) \quad n(t) = \frac{n^{\max}}{1 + e^{-an^{\max}t} \left( \frac{n^{\max}}{n_0} - 1 \right)}.$$

The curve  $n(t)$  given by (1.4) is called logistic curve of the quantity  $n$ . We may consider the function

$$(1.5) \quad \dot{n}(t) = \frac{dn}{dt} = \frac{ae^{-an^{\max}t} (n^{\max})^2 \left( \frac{n^{\max}}{n_0} - 1 \right)}{\left[ 1 + e^{-an^{\max}t} \left( \frac{n^{\max}}{n_0} - 1 \right) \right]^2},$$

which is obtained either deriving the solution (1.4) with respect to the time, or by performing the multiplication on the right-hand side of (1.3). The curve of  $\dot{n}$  is also called logistic curve of the flow  $n$ . Notice that in (1.1) and (1.3) the coefficient  $a$  has dimension

$$(1.6) \quad \dim a = \frac{1}{t},$$

while the unknown  $n(t)$  and the parameter  $n_0$  are dimensionless. The parameter  $a$  is the only quantity that qualifies the collective physical system.

In fig. 1 and 2 we show how the solution  $n(t)$ , given by (1.4), and the solution  $\dot{n}(t)$ , given by (1.5), depend on  $a$ . The figures are given in arbitrary units of  $t$ . If  $a$  is experimentally known, for instance is the coefficient of growth or of decay measured experimentally (in other words, we know a specific property of the physical system under consideration), we can infer from  $a$  a typical time, which will be expressed in the units of time used to evaluate  $a$  itself. For eq. (1.1) we have the doubling time ( $a > 0$ ) or the half time, or mean life ( $a < 0$ ). For the Verhulst equation (1.3) we can define a typical time as follows. Consider the curves of fig. 2 and define the width  $\tau_a$  of the

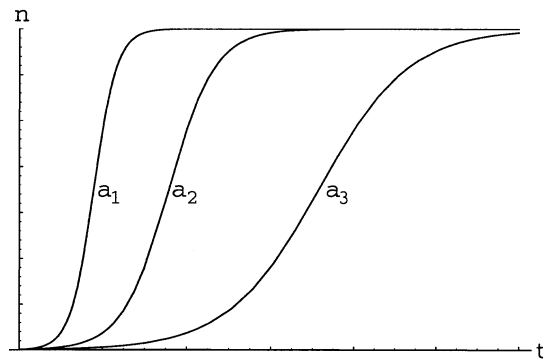


Fig. 1. – This figure shows  $n(t)$  (eq. (1.4)) for different values of the parameter  $a$ . In particular we have chosen  $a_1 = 2 \cdot a_2$ ,  $a_2 = 2 \cdot a_3$ . The variables are given in arbitrary units.

bell-shaped curves  $\dot{n}(t)$  at half height. We can calculate  $\tau_a$  explicitly from (1.5) and get

$$(1.7) \quad \tau_a = \frac{1}{an^{\max}} \frac{3 + 2\sqrt{2}}{3 - 2\sqrt{2}}.$$

Obviously larger  $a$  means steeper growth of  $n(t)$  towards the saturation value  $n^{\max}$  or narrower peak of  $\dot{n}(t)$ .

The above remarks are important in the actual use of the logistic curves, which are rather successful in several problems. For instance they explain and predict the behaviour of the consumption of either renewable or fossil resources by humankind [1].

At this point we may consider the Lotka-Volterra system (1925) [2]. The collective

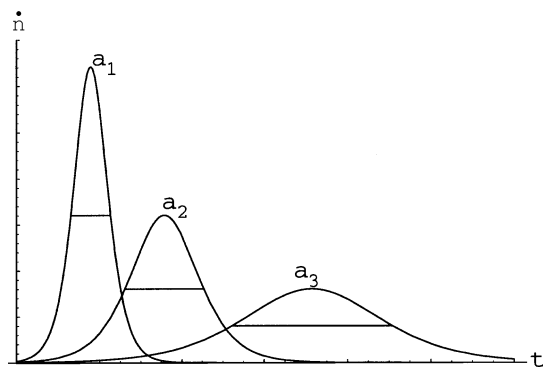


Fig. 2. – This figure shows  $\dot{n}(t)$  (eq. (1.5)) for different values of the parameter  $a$ . In particular we have chosen  $a_1 = 2 \cdot a_2$ ,  $a_2 = 2 \cdot a_3$ . The variables are given in arbitrary units. We have shown on the curves the typical time  $\tau_a$  (eq. (1.7)), defined as the width of the bell-shaped curves  $\dot{n}(t)$  at half height.

dynamics here concerns a prey species  $n(t)$  and a predator species  $p(t)$ . The equations are

$$(1.8) \quad \begin{cases} \dot{n} = an(t) - \alpha n(t) p(t), \\ \dot{p} = -bp(t) + \beta n(t) p(t). \end{cases}$$

The phase space  $n, p$  of (1.8) is the quarter of plane  $n > 0, p > 0$ .

The above equations are asymmetric in a very important way. The prey by itself grows, with the factor  $a$ , and dies with the factor  $-\alpha p(t)$ .

The predator by itself dies, with the factor  $b$ , and grows with the factor  $+\beta n(t)$ .

So the noninteracting prey grows exponentially, while the noninteracting predator dies also exponentially. This asymmetry qualifies the fact of being prey or predator. In principle  $a$  and  $b$  can be determined by measuring the behaviour of the prey alone and the predator alone. We do not touch here the profound issue whether the consideration of a single species alone makes sense or not, because this question touches the problem of evolution, which is outside the scope of the Lotka-Volterra model. For simplicity, we assume here that  $a$  and  $b$  can be determined in principle.

Let us consider the fixed point or equilibrium point of system (1.8). This point is defined by the condition

$$(1.9) \quad \begin{cases} \dot{n} = 0, \\ \dot{p} = 0. \end{cases}$$

We get from (1.9) that the fixed point (with  $n > 0, p > 0$ ) has coordinates

$$(1.10) \quad \begin{cases} \tilde{n} = \frac{b}{\beta}, \\ \tilde{p} = \frac{a}{\alpha}. \end{cases}$$

Notice from (1.10) that the uncoupled solution  $n^{(0)}(t)$  ( $n$  without  $p$ ) and  $p^{(0)}(t)$  ( $p$  without  $n$ ) cannot be reached from the fixed point (1.10) by letting  $\alpha \rightarrow 0, \beta \rightarrow 0$ .

We linearize around the fixed point putting

$$(1.11) \quad \begin{cases} n = \tilde{n} + \xi_n \\ p = \tilde{p} + \xi_p. \end{cases}$$

Inserting (1.11) into (1.8) and retaining only the linear term, in  $\xi_n, \xi_p$ , we get the linear system

$$(1.12) \quad \dot{\vec{\xi}} = A \cdot \vec{\xi},$$

where, obviously,

$$(1.13) \quad \vec{\xi} = \begin{pmatrix} \xi_n \\ \xi_p \end{pmatrix}, \quad A = \begin{pmatrix} 0 & -\frac{\alpha b}{\beta} \\ \frac{a\beta}{\alpha} & 0 \end{pmatrix}.$$

In the linear phase space  $\xi_n, \xi_p$  the flow of  $\vec{\xi}$  is incompressible, or

$$(1.14) \quad \operatorname{div} \vec{\xi} = 0,$$

as we see immediately from (1.12).

We search for a solution of the type  $\xi = \xi_0 e^{\lambda t}$ , and to this purpose we need to diagonalize the matrix  $A$ . This implies the condition

$$(1.15) \quad \det(A - \lambda \mathbf{1}) = 0,$$

which is the secular equation

$$(1.16) \quad \lambda^2 + ab = 0,$$

and the roots are

$$(1.17) \quad \lambda = \pm i\sqrt{ab}.$$

In other words, the linear solution  $\xi_n(t), \xi_p(t)$  in the phase space  $\xi_n, \xi_p$  is a combination of  $\sin \lambda t, \cos \lambda t$ , so the trajectory is a closed curve with period

$$(1.18) \quad \tau = \frac{2\pi}{\sqrt{ab}}.$$

Notice that the period of the solution does not depend on the coupling coefficients  $\alpha$  and  $\beta$ .

The dimensions are

$$\dim a = \frac{1}{t}, \quad \dim b = \frac{1}{t}.$$

In principle  $a$  and  $b$  can be determined experimentally and expressed in a given unit of time. As a consequence (1.18) gives a typical time (the period) of the Lotka-Volterra dynamics.

## 2. – The power input. The constant driving term

Our criticism of the Lotka-Volterra model is that the two species  $n$  and  $p$  are positioned nowhere, they have no relationships with the rest of the Universe. Now any conceivable ecosystem must be positioned on a planet and everything happening on a planet is driven by the flux of energy (in  $\text{W/m}^2$ ) coming from the star (the Sun, for instance) to which the planet belongs.

In this section we consider the case of the constant power input. Moreover we state that the prey (herb) is a certain species of vegetation, the predator (herbivore) is a species feeding on the above vegetation species.

The prey feeds on the solar radiation, using not the total flux, but only that portion that is spanned by the frequency window that is able to produce the photosynthesis. The herb cannot feed on the solar radiation indefinitely, but only until there is radiation available.

For the couple Sun-Earth, we have that the solar flux impinging on a unit surface orthogonal to the direction of the photons is [3]

$$(2.1) \quad \phi^{\max} = (1 - \alpha_e) \mathfrak{S} \approx (1 - 0.3) \cdot 1350 \frac{\text{W}}{\text{m}^2} = 945 \frac{\text{W}}{\text{m}^2},$$

where  $\mathfrak{S}$  is the solar constant (integral of the solar Planck spectrum over all frequencies) and  $\alpha_e = 0.3$  is the average albedo. The photosynthesis window is the following frequency band  $\Delta\nu$  [4]:

$$(2.2) \quad \nu_1 = 0.42 \cdot 10^{15} \text{ s}^{-1} \leq \nu \leq \nu_2 = 0.75 \cdot 10^{15} \text{ s}^{-1}.$$

The portion of the flux (2.1) that belongs to the constraint (2.2) can be calculated [5]. Consequently, we define an effective flux

$$(2.3) \quad \phi_{\Delta}^{\max} = \kappa \phi^{\max}, \quad \kappa = 0.37.$$

In conclusion

$$(2.4) \quad \phi_{\Delta}^{\max} = 0.37 \cdot 945 \frac{\text{W}}{\text{m}^2} = 348.6 \frac{\text{W}}{\text{m}^2}.$$

Let us consider now the prey alone, and the predator alone. The prey alone is represented by  $n(t)$  members, each one characterized by a metabolism  $\phi_0$  (in  $\text{W}/\text{m}^2$ ). So the power processed by the prey is  $\phi_0 \cdot n(t)$ . In the absence of the predator the prey grows according to the logistic equation

$$(2.5) \quad \phi_0 \dot{n}(t) = an(t)(\phi_{\Delta}^{\max} - \phi_0 n(t)), \quad a > 0$$

(this equation is in  $\text{W}/(\text{m}^2 \cdot \text{s})$ ). We may divide eq. (2.5) by  $\phi_0$  and rewrite it as

$$(2.6) \quad \dot{n}(t) = an(t)(n^{\max} - n(t)),$$

where we have put

$$(2.7) \quad n^{\max} = \frac{\phi_{\Delta}^{\max}}{\phi_0}.$$

Notice that  $\phi_{\Delta}^{\max}$  is given by the external power input (the Sun), while  $\phi_0$  is somehow arbitrary; we can either fix our attention on  $\phi_0$  or on  $n^{\max}$ .

The predator, represented by  $p(t)$ , does not feed on the solar flux, it feeds only on the prey. Therefore the predator alone (prey absent) can only die according to the collective law

$$(2.8) \quad \dot{p}(t) = -bp(t), \quad b > 0.$$

We can also define a constant  $\psi_0$ , which is the metabolism of the predator, so that (2.8) can also be rewritten as

$$(2.9) \quad \psi_0 \dot{p}(t) = -b\psi_0 p(t).$$

At this point also  $\psi_0$  is arbitrary. We may consider several cases:

- $\phi_0 > \psi_0$  tree and insect,
- $\phi_0 < \psi_0$  grass and cow,
- etc.

In the following we will adopt  $\phi_0 < \psi_0$  and  $b < a$ . There is a logic in this choice. Larger metabolism implies larger size, and this generally implies death rate  $b$  smaller than growth rate  $a$ . This means qualitatively that the larger predator dies at a slower rate with respect to the prey growth rate [6].

When prey and predator couple, we have only one acceptable scheme of coupling, which is dictated by the energy conservation:

$$(2.10) \quad \begin{cases} \dot{n} = an \left( \frac{\phi_{\Delta}^{\max}}{\phi_0} - p \frac{\psi_0}{\phi_0} - n \right) - \alpha np, \\ \dot{p} = -bp + \beta p \left( \frac{\phi_0}{\psi_0} n - p \right). \end{cases}$$

The term  $\phi_{\Delta}^{\max} - p\psi_0 - n\phi_0$  is the saturation factor for the prey population power  $\phi_0 n(t)$ , while the growth of the predator power  $\psi_0 p(t)$  saturates at the value  $\phi_0 n(t)$ .

In (2.10) the dimensions are

$$[a] = [b] = [\alpha] = [\beta] = t^{-1}.$$

In this section we study the mathematical properties of (2.10). Let us first examine the fixed point of system (2.10). The fixed point has coordinates  $\tilde{n}$  and  $\tilde{p}$  solution of

$$(2.11) \quad \begin{cases} \dot{n} = 0, \\ \dot{p} = 0, \end{cases}$$

or

$$(2.12) \quad \begin{cases} an \left( \frac{\phi_{\Delta}^{\max}}{\phi_0} - p \frac{\psi_0}{\phi_0} - n \right) - \alpha np = 0, \\ -bp + \beta p \left( \frac{\phi_0}{\psi_0} n - p \right) = 0. \end{cases}$$

We look for the nontrivial solution  $\tilde{n} > 0, \tilde{p} > 0$ , so that we write

$$(2.13) \quad \begin{cases} a \left( \frac{\phi_{\Delta}^{\max}}{\phi_0} - p \frac{\psi_0}{\phi_0} - n \right) - \alpha p = 0, \\ -b + \beta \left( \frac{\phi_0}{\psi_0} n - p \right) = 0. \end{cases}$$

From (2.13) we get

$$(2.14) \quad \left\{ \begin{array}{l} \tilde{n} = \frac{\frac{b}{\beta} \left( \frac{\alpha}{a} + \frac{\psi_0}{\phi_0} \right) + \frac{\phi_{\Delta}^{\max}}{\phi_0}}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}}, \\ \tilde{p} = \frac{\left( -\frac{b}{\beta} + \frac{\phi_{\Delta}^{\max}}{\psi_0} \right)}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}}. \end{array} \right.$$

The condition  $\tilde{p} > 0$  imposes the constraint

$$(2.15) \quad \beta > b \frac{\psi_0}{\phi_{\Delta}^{\max}} = \beta_{\min},$$

while the condition  $\tilde{n} > 0$  holds for every  $\alpha > 0$ .

Notice that the explicit expression (2.14) contains the inequality

$$(2.16) \quad \tilde{p} \psi_0 \leq \tilde{n} \phi_0,$$

and also the inequality

$$(2.17) \quad \tilde{n} \phi_0 + \tilde{p} \psi_0 \leq \phi_{\Delta}^{\max}.$$

Equation (2.17) comes by direct application of the constraint (2.15), in fact

$$(2.18) \quad \begin{aligned} \tilde{n} \phi_0 + \tilde{p} \psi_0 &= \frac{\frac{b}{\beta} \left( \frac{\alpha}{a} + \frac{\psi_0}{\phi_0} \right) + \frac{\phi_{\Delta}^{\max}}{\phi_0}}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}} \phi_0 + \frac{-\frac{b}{\beta} + \frac{\phi_{\Delta}^{\max}}{\psi_0}}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}} \psi_0 = \\ &= \frac{\frac{b}{\beta} \left( \frac{\alpha}{a} \phi_0 + \psi_0 \right) + \phi_{\Delta}^{\max} - \frac{b}{\beta} \psi_0 + \phi_{\Delta}^{\max}}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}} = \frac{\frac{b}{\beta} \frac{\alpha}{a} \phi_0 + 2\phi_{\Delta}^{\max}}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}} \leq \\ &\leq \frac{\phi_{\Delta}^{\max} \frac{\alpha}{a} \frac{\phi_0}{\psi_0} + 2\phi_{\Delta}^{\max}}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}} = \phi_{\Delta}^{\max}. \end{aligned}$$



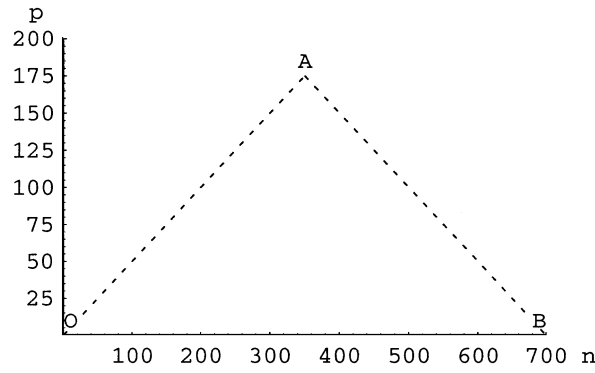


Fig. 3. – Domain of the fixed point in the phase space  $n, p$ , where the segment AB belongs to the line  $p = -\frac{\phi_0}{\psi_0} n + \frac{\phi_A^{\max}}{\psi_0}$  and the segment OA belongs to the line  $p = \frac{\phi_0}{\psi_0} n$ . The point A has coordinates  $\left(\frac{\phi_A^{\max}}{2\phi_0}, \frac{\phi_A^{\max}}{2\psi_0}\right)$ . If we choose  $\phi_0 = 0.498 \frac{W}{m^2}$  and  $\psi_0 = 2\phi_0 = 0.996 \frac{W}{m^2}$ , we obtain  $\tilde{n}^{\max} = \frac{\phi_A^{\max}}{\phi_0} = 700$  and  $\tilde{p}^{\max} = p_A = 175$ .

Therefore the domain of the fixed point  $\tilde{n}, \tilde{p}$ , in the phase space  $n, p$  is the triangle OAB (fig. 3), where the segment AB belongs to the line

$$p = -\frac{\phi_0}{\psi_0} n + \frac{\phi_A^{\max}}{\psi_0}$$

and the segment OA belongs to the line

$$p = \frac{\phi_0}{\psi_0} n.$$

The point A has coordinates

$$n_A = \frac{\phi_A^{\max}}{2\phi_0}, \quad p_A = \frac{\phi_A^{\max}}{2\psi_0}.$$

We adopt here and in the following the arbitrary choice

$$\phi_0 = 0.498 \frac{W}{m^2},$$

so that

$$\tilde{n}^{\max} = n^{\max} = \frac{\phi_A^{\max}}{\phi_0} = 700,$$

$$\psi_0 = 2\phi_0 = 0.996 \frac{W}{m^2},$$

so that

$$\tilde{p}^{\max} = p_A = 175 .$$

The input term  $\phi_{\Delta}^{\max}$  and the parameters  $\phi_{\Delta}^{\max}$ ,  $\phi_0$ ,  $\psi_0$ ,  $a$  and  $b$  have been assumed to be given, while the coupling parameters  $\alpha$  and  $\beta$  are in principle free.

In general we may define the solar efficiency of the prey-predator system by

$$(2.19) \quad \eta = \frac{n\phi_0 + p\psi_0}{\phi_{\Delta}^{\max}} .$$

We have

$$\eta(\tilde{n}, \tilde{p}) \leq 1 ,$$

by virtue of (2.18). Clearly,  $\eta = 1$  for values of  $n, p$  lying on the segment AB; and  $\eta = 0$  for  $n = 0, p = 0$ . The plane  $\eta(\tilde{n}, \tilde{p})$  is shown in fig. 4.

We analyze now the temporal evolution of a volume in the phase space in the neighbourhood of the fixed point. We know that for a differential system  $\dot{x} = \vec{v}(x)$  (where  $\vec{v}(x(t))$  and  $x(t)$  are vectors in the phase space  $x$ ), if we call  $\Delta\tau$  a volume element surrounding a certain value  $\vec{x}_0$ , we have  $\frac{1}{\Delta\tau} \frac{\partial(\Delta\tau)}{\partial t} = \text{div } \vec{v}$  [7]. In our case, we have

$$(2.20) \quad \text{div } \vec{v} = \left\{ \frac{\partial \dot{n}}{\partial n} + \frac{\partial \dot{p}}{\partial p} \right\}_{n=\tilde{n}; p=\tilde{p}} =$$

$$= a \left( \frac{\phi_{\Delta}^{\max}}{\phi_0} - \tilde{p} \frac{\psi_0}{\phi_0} - \tilde{n} \right) - \alpha \tilde{p} - a \tilde{n} - b + \beta \left( \frac{\phi_0}{\psi_0} \tilde{n} - \tilde{p} \right) - \beta \tilde{p} = - a \tilde{n} - \beta \tilde{p} < 0 ,$$

in the last step we have used (2.13). Thanks to this result we can say that the system of equations (2.10) is dissipative.

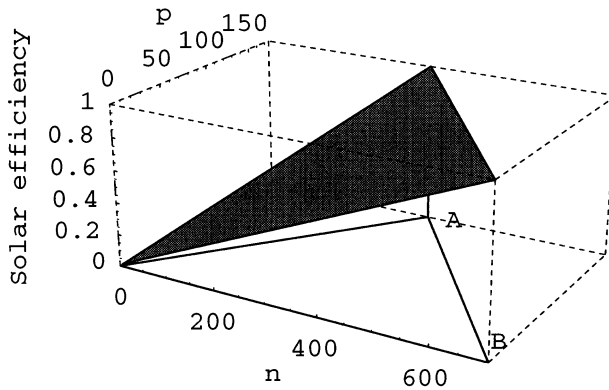


Fig. 4. - The efficiency  $\eta(\tilde{n}, \tilde{p}) = \frac{\tilde{n}\phi_0 + \tilde{p}\psi_0}{\phi_{\Delta}^{\max}}$  calculated as a function of  $\tilde{n}, \tilde{p}$ . The domain of the fixed point in the phase space  $n, p$  is the triangle drawn in fig. 3. In particular, for  $\tilde{n}$  and  $\tilde{p}$  lying on the line  $p = -\frac{\phi_0}{\psi_0}n + \frac{\phi_{\Delta}^{\max}}{\psi_0}$ , namely AB, we have  $\eta = 1$ ; for  $\tilde{n} = 0$  and  $\tilde{p} = 0$  we have  $\eta = 0$ .

We have seen in the preceding session that the fixed point of the Lotka-Volterra system is a center. We show now that the fixed point of our system (2.10) is a sink. To this purpose we analyze system (2.10) in the linear approximation.

Let us put

$$(2.21) \quad \begin{cases} \dot{n} = f_n(n, p), \\ \dot{p} = f_p(n, p), \end{cases}$$

and

$$(2.22) \quad n = \tilde{n} + \xi_n, \quad p = \tilde{p} + \xi_p.$$

The linear system is

$$(2.23) \quad \begin{cases} \dot{\xi}_n = \left( \frac{\partial f_n}{\partial n} \right)_{\tilde{n}, \tilde{p}} \xi_n + \left( \frac{\partial f_n}{\partial p} \right)_{\tilde{n}, \tilde{p}} \xi_p, \\ \dot{\xi}_p = \left( \frac{\partial f_p}{\partial n} \right)_{\tilde{n}, \tilde{p}} \xi_n + \left( \frac{\partial f_p}{\partial p} \right)_{\tilde{n}, \tilde{p}} \xi_p. \end{cases}$$

Performing the partial derivatives, we find immediately

$$(2.24) \quad \begin{cases} \dot{\xi}_n = \left( a \frac{\phi_{\Delta}^{\max}}{\phi_0} - 2a\tilde{n} - a\tilde{p} - a \frac{\psi_0}{\phi_0} \tilde{p} \right) \xi_n - \left( \alpha\tilde{n} + a \frac{\psi_0}{\phi_0} \tilde{n} \right) \xi_p, \\ \dot{\xi}_p = \beta\tilde{p} \frac{\phi_0}{\psi_0} \xi_n + \left( \beta\tilde{n} \frac{\phi_0}{\psi_0} - b - 2\beta\tilde{p} \right) \xi_p. \end{cases}$$

We can write it in a matrix form:

$$(2.25) \quad \dot{\vec{\xi}} = A \cdot \vec{\xi},$$

where

$$A = \begin{pmatrix} -a \frac{\frac{b}{\beta} \left( \frac{\alpha}{a} + \frac{\psi_0}{\phi_0} \right) + \frac{\phi_{\Delta}^{\max}}{\phi_0}}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}} & -a \left( \frac{\alpha}{a} + \frac{\psi_0}{\phi_0} \right) \frac{\frac{b}{\beta} \left( \frac{\alpha}{a} + \frac{\psi_0}{\phi_0} \right) + \frac{\phi_{\Delta}^{\max}}{\phi_0}}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}} \\ \beta \frac{\phi_0}{\psi_0} \frac{\frac{\phi_{\Delta}^{\max}}{\psi_0} - \frac{b}{\beta}}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}} & -\beta \frac{\frac{\phi_{\Delta}^{\max}}{\psi_0} - \frac{b}{\beta}}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}} \end{pmatrix},$$

in  $A$  we have used for  $\tilde{n}$  and  $\tilde{p}$  the explicit expressions given in (2.14). We study now the two eigenvalues of the matrix  $A$  written above. To this purpose we write the secular equation

$$(2.26) \quad \det(A - \lambda \mathbf{1}) = 0,$$

from which we get

$$(2.27) \quad \lambda_{1,2} = \frac{1}{2 \left( 2 + \frac{\alpha \phi_0}{a \psi_0} \right)} \left\{ -a \left( \frac{\phi_{\Delta}^{\max}}{\phi_0} + \frac{\psi_0 b}{\phi_0 \beta} + \frac{\beta \phi_{\Delta}^{\max}}{a \psi_0} + \frac{\alpha b}{a \beta} - \frac{b}{a} \right) \pm \right. \\ \left. \pm \left[ a^2 \left( \frac{\phi_{\Delta}^{\max}}{\phi_0} + \frac{\psi_0 b}{\phi_0 \beta} + \frac{\beta \phi_{\Delta}^{\max}}{a \psi_0} + \frac{\alpha b}{a \beta} - \frac{b}{a} \right)^2 - \right. \right. \\ \left. \left. - 4a\beta \left( \frac{\phi_{\Delta}^{\max}}{\psi_0} - \frac{b}{\beta} \right) \left( \frac{\phi_{\Delta}^{\max}}{\phi_0} + \frac{\alpha b}{a \beta} + \frac{\psi_0 b}{\phi_0 \beta} \right) \left( \frac{\alpha \phi_0}{a \psi_0} + 2 \right) \right]^{1/2} \right\}$$

or in short

$$(2.28) \quad \lambda_{1,2} = -\lambda^{(0)} \pm \lambda^{(1)},$$

where

$$(2.29) \quad \left\{ \begin{array}{l} \lambda^{(0)} = \frac{1}{2 \left( 2 + \frac{\alpha \phi_0}{a \psi_0} \right)} \left\{ a \left( \frac{\phi_{\Delta}^{\max}}{\phi_0} + \frac{\psi_0 b}{\phi_0 \beta} + \frac{\beta \phi_{\Delta}^{\max}}{a \psi_0} + \frac{\alpha b}{a \beta} - \frac{b}{a} \right) \right\}, \\ \lambda^{(1)} = \frac{1}{2 \left( 2 + \frac{\alpha \phi_0}{a \psi_0} \right)} \left[ a^2 \left( \frac{\phi_{\Delta}^{\max}}{\phi_0} + \frac{\psi_0 b}{\phi_0 \beta} + \frac{\beta \phi_{\Delta}^{\max}}{a \psi_0} + \frac{\alpha b}{a \beta} - \frac{b}{a} \right)^2 - \right. \\ \left. - 4a\beta \left( \frac{\phi_{\Delta}^{\max}}{\psi_0} - \frac{b}{\beta} \right) \left( \frac{\phi_{\Delta}^{\max}}{\phi_0} + \frac{\alpha b}{a \beta} + \frac{\psi_0 b}{\phi_0 \beta} \right) \left( \frac{\alpha \phi_0}{a \psi_0} + 2 \right) \right]^{1/2}. \end{array} \right.$$

We see that  $\lambda^{(0)}$  is positive because

$$(2.30) \quad \frac{\beta \phi_{\Delta}^{\max}}{a \psi_0} > \frac{b}{a},$$

thanks to (2.15). Moreover,  $\lambda^{(1)}$  is either positive and smaller than  $\lambda^{(0)}$  or imaginary, again thanks to (2.15). The net result is that the fixed point is a sink with either two straight directions of approach, in the first case, or a spiral, in the second case. In conclusion, every trajectory  $n(t)$ ,  $p(t)$  originated at  $n_0$ ,  $p_0$  for  $t = 0$  in the phase space, for a given value of  $\alpha$  and  $\beta$ , will fall in the point  $\tilde{n}(\alpha, \beta)$ ,  $\tilde{p}(\alpha, \beta)$  lying in the triangle of fig. 3.

Given two points, namely  $(n_0, p_0)$  for  $t = 0$  and  $(\tilde{n}, \tilde{p})$  for  $t = \infty$ , the linear trajectory and the nonlinear trajectory joining them can be close to each other or distant from each other depending on the  $\alpha, \beta$  chosen. This fact is nontrivial and implies the understanding of the functional relationship  $\alpha, \beta \rightarrow \tilde{n}, \tilde{p}$ .

Now we study how the fixed point  $\tilde{n}, \tilde{p}$  moves in the allowed triangular domain in phase space when the parameters  $\alpha, \beta$  span their own domain:

$$(2.31) \quad \beta > \beta_{\min}, \quad \alpha > 0.$$

Notice that the map  $\alpha, \beta \rightarrow \tilde{n}, \tilde{p}$  is not a homeomorphism, because the function  $\tilde{p}(\alpha, \beta)$  is not single valued. In order to analyze the relationship  $\alpha, \beta \rightarrow \tilde{n}, \tilde{p}$ , we remark that the consideration of the parameters  $\alpha$  and  $\beta$  as two independent variables is not realistic. In fact  $\beta$  contains the information of how the population  $p(t)$  grows by feeding on  $n(t)$  and  $\alpha$  contains the information of how the population  $n(t)$  is diminished by the same cause. It makes sense to consider a linear relationship between  $\alpha$  and  $\beta$  of the kind

$$(2.32) \quad \beta - \beta_{\min} = \beta' = k\alpha.$$

In such a way we scan the domain  $\beta' > 0, \alpha > 0$  by straight lines.

From (2.32) we may define a parameter  $\gamma$  in this way:

$$(2.33) \quad k = \frac{\gamma}{1 - \gamma},$$

or

$$(2.34) \quad \gamma = \frac{\beta'}{\beta' + \alpha},$$

and we see that  $\gamma$  can be considered as a measure of the efficiency of the predator. In fact  $\gamma \rightarrow 0$  means  $\beta' \rightarrow 0$  for a given  $\alpha > 0$ , which means that the predator wastes its prey with a rate  $\alpha$  without any benefit (for  $\beta' \rightarrow 0$  the predator equation has no growth contribution); for  $\gamma \rightarrow 1$ , we have that for a given  $\beta', \alpha \rightarrow 0$ , that is the predator has a benefit without a loss of a prey. On the other hand, we have previously defined a solar efficiency of the prey-predator system:

$$(2.35) \quad \eta = \frac{n\phi_0 + p\psi_0}{\phi_A^{\max}} = \eta(\alpha, \gamma).$$

It is therefore quite interesting to see how  $\eta$  depends on  $\alpha$  for various values of  $\gamma$ . In conclusion we study the motion of the fixed point  $\tilde{n}, \tilde{p}$  as a function of  $\alpha$ , for various values of  $\gamma$ .

Remember that in this section system (2.10) contains a typical scale for the power:  $\phi_A^{\max}$ , which is given from the outside; conversely  $\psi_0$  and  $\phi_0$  are properties of the chosen species, and can be chosen in such a way that the domain of the fixed point in the phase space, the triangle of fig. 3, is determined. On the opposite, there is no external time scale, no privileged unit of the time  $t$  and consequently no privileged values of  $a$  and  $b$ . We have given a reasonable guess to relate  $\phi_0, \psi_0$  to  $a, b$ , namely  $a$  larger than  $b$  implies  $\psi_0$  larger than  $\phi_0$ . To fix the ideas, we chose for the numerical calculations

$$(2.36) \quad \psi_0 = 2\phi_0, \quad a = 2b.$$

This is all we can say. At the end, the parameter  $a$  remains undetermined and consequently we let the remaining parameter  $a$  be specified simply in units of  $a$ . This is

what we will do in the calculations that follow. Having established the linear relationship (2.32), or

$$(2.37) \quad \beta = \beta_{\min} + \frac{\gamma}{1 - \gamma} \alpha,$$

we rewrite here the two functions  $\tilde{n}, \tilde{p}$  (eq. (2.14)) as follows:

$$(2.38) \quad \left\{ \begin{aligned} \tilde{n} = \tilde{n}(\alpha, \gamma) &= \frac{\frac{b}{\beta_{\min} + \frac{\gamma}{1 - \gamma} \alpha} \left( \frac{\alpha}{a} + \frac{\psi_0}{\phi_0} \right) + \frac{\phi_{\Delta}^{\max}}{\phi_0}}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}}, \\ \tilde{p} = \tilde{p}(\alpha, \gamma) &= \frac{\left( -\frac{b}{\beta_{\min} + \frac{\gamma}{1 - \gamma} \alpha} + \frac{\phi_{\Delta}^{\max}}{\psi_0} \right)}{2 + \frac{\alpha}{a} \frac{\phi_0}{\psi_0}}. \end{aligned} \right.$$

We find that

$$(2.39) \quad \frac{d\tilde{n}}{d\alpha} < 0, \quad \gamma \text{ fixed},$$

while  $\tilde{p}(\alpha, \gamma)$  has a maximum at a certain value  $\alpha_0$ , solution of

$$(2.40) \quad \frac{d\tilde{p}}{d\alpha} = 0, \quad \gamma \text{ fixed}.$$

The root of (2.40) is

$$(2.41) \quad \alpha = \alpha_0(\gamma) = \frac{2a\psi_0}{\phi_0} \left( \frac{b\phi_0(1 - \gamma)}{2a\gamma\phi_{\Delta}^{\max}} \right)^{1/2}.$$

Let us consider now

$$(2.42) \quad \eta = \eta(\tilde{n}, \tilde{p}) = \eta(\alpha, \gamma).$$

We find that

$$(2.43) \quad \frac{d\eta}{d\alpha} < 0, \quad \text{for } \alpha > 0, \quad \gamma \text{ fixed},$$

and that  $\eta(\alpha, \gamma)$  has a flex point

$$(2.44) \quad \frac{d^2\eta}{d\alpha^2} = 0,$$

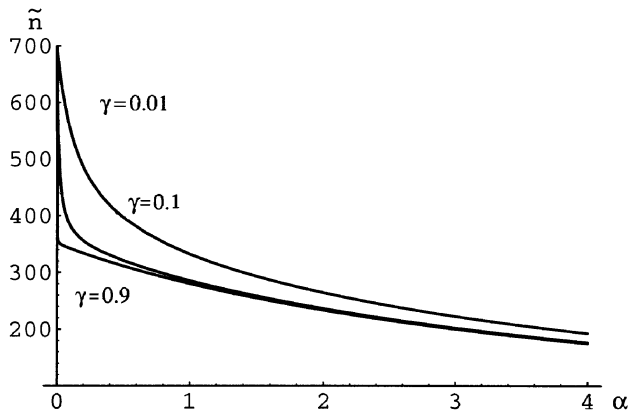


Fig. 5. – In this figure we show the behaviour of  $\tilde{n}$  as a function of  $\alpha$  for  $\alpha$  in the interval  $0 < \alpha < 4a$  and for three selected values of  $\gamma$ :  $\gamma = 0.01$ ,  $\gamma = 0.1$ ,  $\gamma = 0.9$ . The reference case  $\gamma = 0.5$  is very close to the curve corresponding to  $\gamma = 0.9$ .

at a value  $\alpha_1$ , which can be calculated explicitly

$$(2.45) \quad \alpha = \alpha_1 = \frac{2a\psi_0}{\phi_0} \frac{\left(\frac{b(1-\gamma)\phi_0}{2a\gamma\phi_{\Delta}^{\max}}\right)^{1/3} + \left(\frac{2a\gamma\phi_{\Delta}^{\max}}{b(1-\gamma)\phi_0}\right)^{1/3} - 1}{1 + \frac{2a\gamma\phi_{\Delta}^{\max}}{b(1-\gamma)\phi_0}} .$$

It is possible to show that

$$(2.46) \quad \alpha_0 > \alpha_1 > 0 ,$$

for any value of  $\gamma$ .

After these preliminaries, we possess the background necessary to understand the graphs that follow. In fig. 5 we show  $\tilde{n}$  as a function of  $\alpha$ , for  $\alpha$  in the interval

$$(2.47) \quad 0 < \alpha < 4a ,$$

and for three selected values of  $\gamma$ :

$$(2.48) \quad \begin{cases} \gamma = 0.01, & \gamma = 0.1, & \gamma = 0.9, \\ k = 0.01, & k = 0.11, & k = 9. \end{cases}$$

Figure 6 shows the behaviour of  $\tilde{p}$  in the same interval of  $\alpha$  values (2.47) and for the same three selected values of  $\gamma$  (2.48). We see that the peak value of  $\tilde{p}$  increases for  $\gamma$  approaching the limit value 1.

Figures 5 and 6 are combined in fig. 7, where we see the position of the fixed point  $\tilde{n}, \tilde{p}$  in the triangular domain of the phase space  $n, p$ .

The relationship between the global solar efficiency  $\eta$  and the predator efficiency  $\gamma$  is shown in fig. 8. In this figure we have chosen for  $\alpha$  the value  $\alpha = \alpha_0(\gamma)$ , namely the

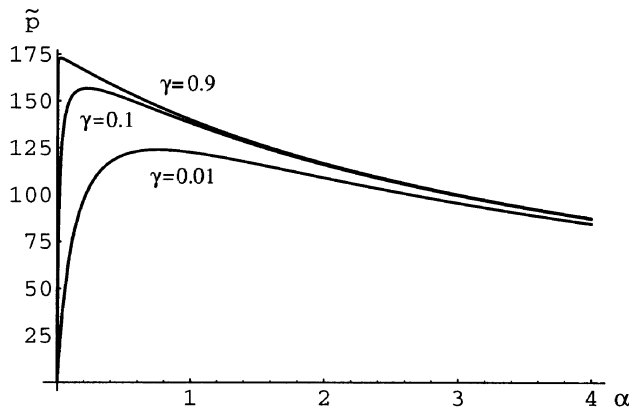


Fig. 6. – In this figure we show the behaviour of  $\tilde{p}$  as a function of  $\alpha$ , for  $\alpha$  in the interval  $0 < \alpha < 4a$  and for the three selected values of  $\gamma$  (2.48). We see that the peak value of  $\tilde{p}$  increases for  $\gamma$  approaching the limit value 1. The reference case  $\gamma = 0.5$  is very close to the curve corresponding to  $\gamma = 0.9$ .

value that maximizes the predator population:

$$(2.49) \quad \eta(\alpha_0, \gamma) = \eta(\alpha_0(\gamma), \gamma).$$

We are finally ready to discuss the flow  $n(t), p(t)$  of the equation of motion (2.10). In the phase space every trajectory is a finite line joining  $n(t=0), p(t=0)$  and  $n(t=\infty), p(t=\infty)$  for a given choice of  $\alpha, \gamma$  (fig. 9). In general, we may assume that the parameters  $\phi_0, \psi_0, a, b$  can be estimated phenomenologically, but  $\alpha$  and  $\gamma$  remain unknown. Nevertheless, the preceding discussion enables us to relate each couple  $\alpha, \gamma$

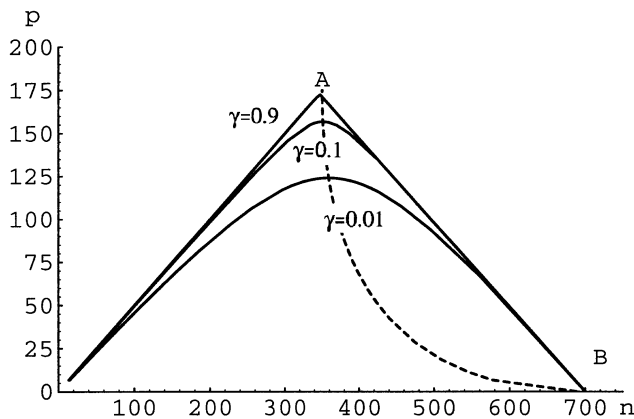


Fig. 7. – In this figure we see the position of the fixed point  $\tilde{n}, \tilde{p}$  in the triangular domain of the phase space  $n, p$ . The running parameter is  $\alpha$ . For  $\alpha = 0, \tilde{n} = 700, \tilde{p} = 0$  (namely point B). For  $\alpha \rightarrow \infty$ , we see from (2.14) that  $\tilde{n}, \tilde{p} \rightarrow 0$ . Notice that the curve corresponding to  $\gamma = 0.9$  is practically indistinguishable from the segments BA, AO. In the figure the ensemble of the points  $\tilde{n}, \tilde{p}^{\max}$ , where  $\tilde{n} = \tilde{n}(\alpha_0(\gamma))$   $\tilde{p}^{\max} = \tilde{p}(\alpha_0(\gamma))$  is also shown (dashed line). The reference case  $\gamma = 0.5$  is very close to the curve corresponding to  $\gamma = 0.9$ .



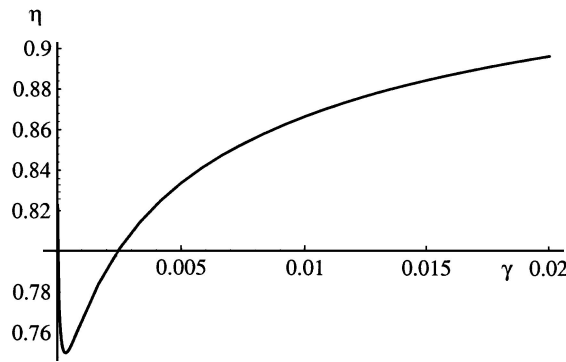


Fig. 8. – In this figure we show the solar efficiency  $\eta$  as a function of  $\gamma$ , having chosen for  $\alpha$  the value  $\alpha = \alpha_0(\gamma)$ , namely the value that maximizes the predator population. Notice that, due to this particular choice of  $\alpha$ ,  $\eta \rightarrow 1$  for  $\gamma \rightarrow 0$  and for  $\gamma \rightarrow 1$ , and the function  $\eta(\gamma)$  has a minimum for  $\gamma = \left(2 \frac{\alpha}{b} \frac{\phi_A^{\max}}{\phi_0} + 1\right)^{-1} = 3.57 \cdot 10^{-4}$ . The choice  $\gamma \rightarrow 0$  means no predator, and in this case the prey saturates the solar flux,  $\eta = 1$ . As the predator comes in, and begins to interact with low efficiency  $\gamma$ , the solar efficiency  $\eta$  drops to a minimum and then grows with  $\gamma$ . We remark that, from the definition of  $\gamma$  (2.33), the limit values  $\gamma \rightarrow 0$  and  $\gamma \rightarrow 1$  are unrealistic. The reference case  $\gamma = 0.5$  corresponds to  $\eta = 0.98$ .

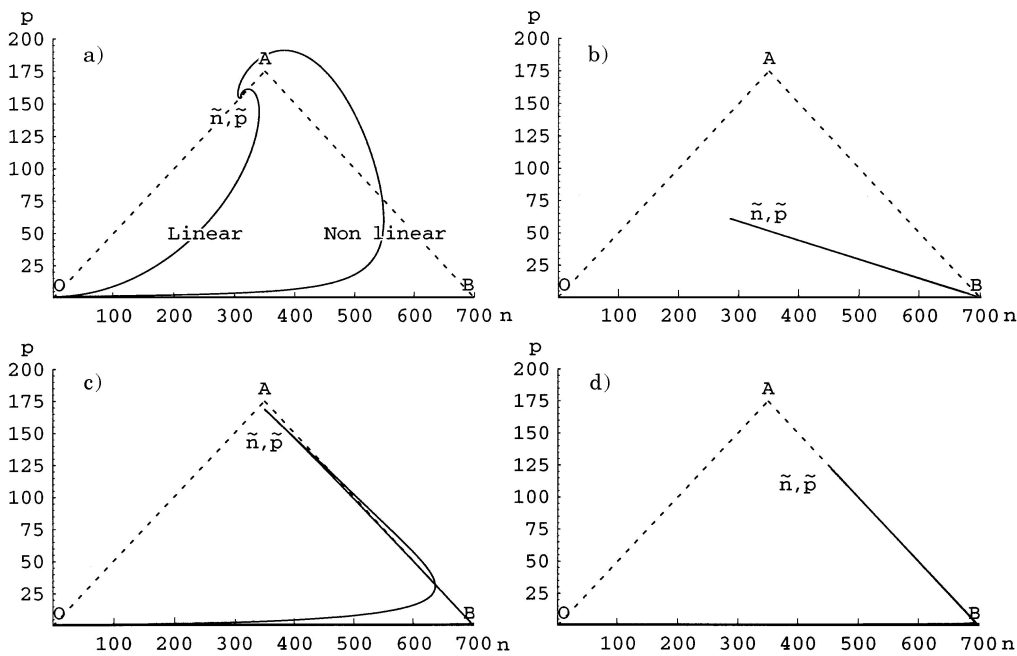


Fig. 9. – Particular trajectories in the phase space  $n, p$ , solutions of the system (2.10) and of the linearized system (2.22), starting at the point  $n_0 = p_0 = 1$  at  $t = 0$ , and ending at the point  $\tilde{n}(\alpha, \gamma)$ ,  $\tilde{p}(\alpha, \gamma)$  at  $t = \infty$ . a)  $\alpha = 20\alpha_0, \gamma = 0.9$ ; b)  $\alpha = 2\alpha_0, \gamma = 0.001$ ; c)  $\alpha = \alpha_0, \gamma = 0.5$ ; d)  $\alpha = 0.05\alpha_0, \gamma = 0.5$ . Notice that the spiralization in a) is due to the complex conjugate eigenvalues. In b) and d) the linear trajectory is almost indistinguishable from the non linear one.

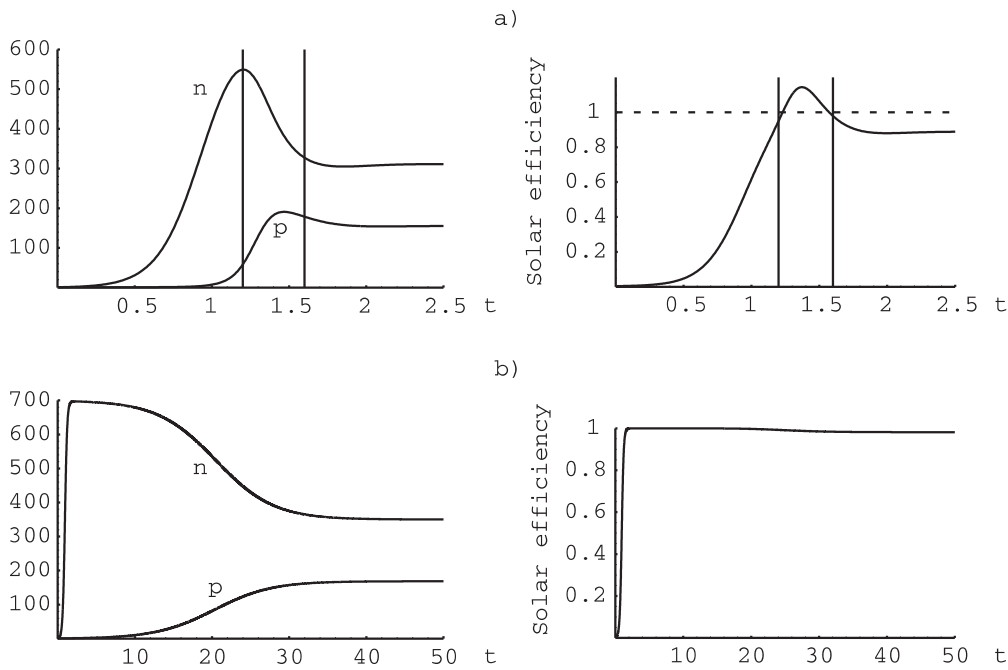


Fig. 10. – In the figures on the left-hand side we show the approach to the asymptotic value of  $n(t)$  and  $p(t)$  corresponding to different values of  $\alpha$  and  $\gamma$ , solutions of the system (2.10), starting at the point  $n_0 = p_0 = 1$  at  $t = 0$ , and ending at the point  $\tilde{n}(\alpha, \gamma), \tilde{p}(\alpha, \gamma)$  at  $t = \infty$ . The figures on the right-hand side show the efficiency  $\eta$ . a)  $\alpha = 20\alpha_0, \gamma = 0.9$ ; b)  $\alpha = \alpha_0, \gamma = 0.5$ . The time is expressed in units of  $10^{-2}a^{-1}$ .

to a position of the end point  $\tilde{n}, \tilde{p}$  in the triangle OAB. Therefore, in principle, the experimental observation of the trajectory  $n_0, p_0 \rightarrow \tilde{n}, \tilde{p}$  gives a method for identifying  $\alpha$  and  $\gamma$ .

The following figures are divided into two groups. In fig. 10 we study the development of the system when the initial condition is the minimum seed:  $n_0 = 1, p_0 = 1$ . The behaviour of the various solutions belonging to different couples  $\alpha, \gamma$  has these features:

- the prey develops quickly, tending to its maximum value if the coupling  $\alpha$  is small compared to  $a$ , then the predator takes over, reduces the prey number and the two species together tend to the end point;
- when the coupling maximizes the predator ( $\alpha = \alpha_0(\gamma)$ ), the corresponding  $\tilde{n}, \tilde{p}$  values lie roughly at the center line of the triangle ( $\gamma$  not too small), see fig. 7;
- for  $\alpha > \alpha_0$  the end point lies on the left sector of the triangle.

In fig. 11 we study the development of the system when the initial condition is the fully grown prey  $n_0 = 698$  and the predator comes in as a seed  $p_0 = 1$ . With  $n_0 = 698$  and  $p_0 = 1$ , we have an initial state that satisfies the energy balance:  $698\phi_0 + 1\psi_0 = \phi_A^{\max}$ .

It is interesting to remark that our model predicts for a certain  $\alpha$  and  $\gamma$  a transient of overgrowth, namely an interval of time in which the power of the system is larger

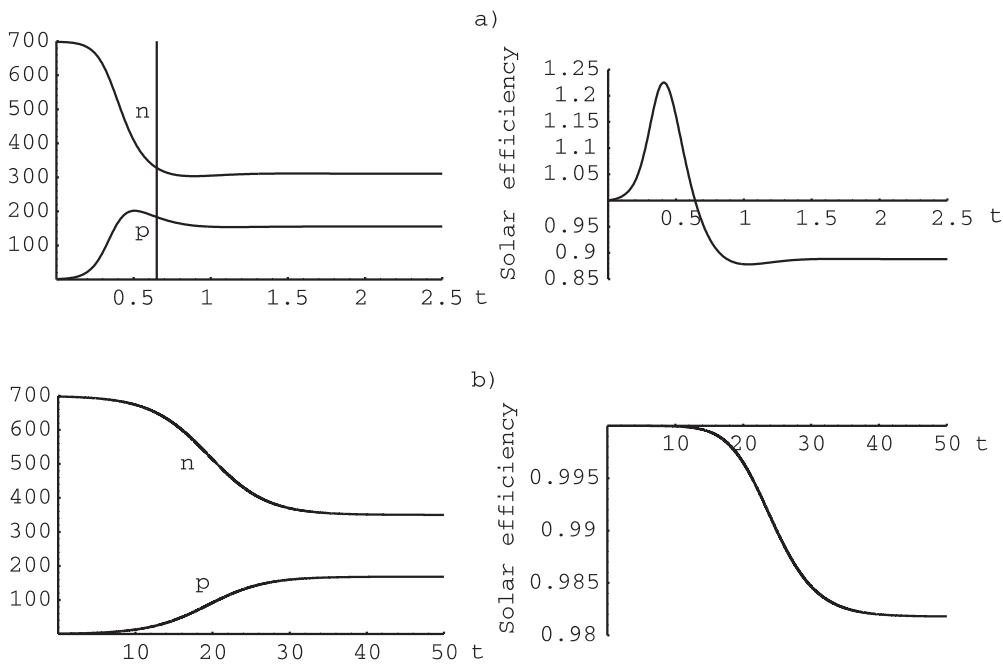


Fig. 11. – In the figures on the left-hand side we show the approach to the asymptotic value of  $n(t)$  and  $p(t)$  corresponding to different values of  $\alpha$  and  $\gamma$ , solutions of the system (2.10), starting at the point  $n_0 = 698, p_0 = 1$  at  $t = 0$ , and ending at the point  $\tilde{n}(\alpha, \gamma), \tilde{p}(\alpha, \gamma)$  at  $t = \infty$ . The figures on the right-hand side show the efficiency  $\eta$ . a)  $\alpha = 20\alpha_0, \gamma = 0.9$ ; b)  $\alpha = \alpha_0, \gamma = 0.5$ . The time is expressed in units of  $10^{-2} \text{a}^{-1}$ .

than the solar flux:  $\phi_0 n(t) + \psi_0 p(t) > \phi_{\Delta}^{\text{max}}$ . The overgrowth appears in the strong-coupling case,  $\alpha = 20\alpha_0$  and not in the reference case  $\alpha = \alpha_0$ .

From fig. 10 and 11 we observe that the time necessary for  $n(t)$  and  $p(t)$  to get very close to  $\tilde{n}$  and  $\tilde{p}$  is of the order of  $\sim 10^{-2} \text{a}^{-1}$  in the strong-coupling case  $\alpha = 20\alpha_0$  and is of the order of  $\sim 30 \cdot 10^{-2} \text{a}^{-1}$  in the reference case  $\alpha = \alpha_0$ . We can have a deeper

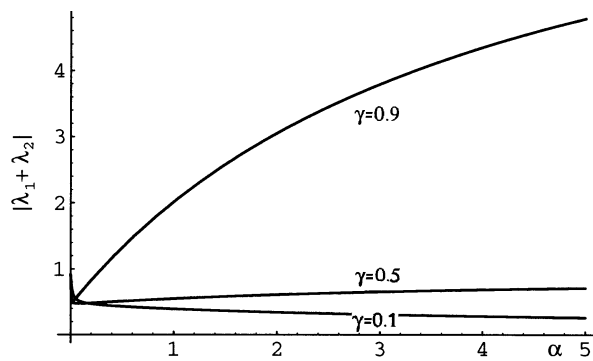


Fig. 12. –  $|\lambda_1 + \lambda_2|$  as a function of  $\alpha$  (in units of  $\text{a}$ ) for the values of  $\gamma = 0.9, 0.5, 0.1$ .  $|\lambda_1 + \lambda_2|$  large means short transient time,  $|\lambda_1 + \lambda_2|$  small means long transient time.

insight into this fact by considering the behaviour of the roots  $\lambda_1$  and  $\lambda_2$  of the linearized system (2.22) which governs the exponential decay of the solution to the asymptotic value  $\tilde{n}, \tilde{p}$ . Let us consider

$$(2.50) \quad |\lambda_1 + \lambda_2| = \frac{1}{2 + \frac{\alpha \phi_0}{a \psi_0}} \left\{ a \left( \frac{\phi_{\Delta}^{\max}}{\phi_0} + \frac{\psi_0 b}{\phi_0 \beta} + \frac{\beta \phi_{\Delta}^{\max}}{a \psi_0} + \frac{\alpha b}{a \beta} - \frac{b}{a} \right) \right\},$$

this quantity is real and negative and has dimension  $t^{-1}$ .  $|\lambda_1 + \lambda_2|$  large means short transient time,  $|\lambda_1 + \lambda_2|$  small means long transient time. In fig. 12 we show the plot of eq. (2.50).

We conclude this section with a remark on “the good predator”.

Nature comes in such a way that there are preys and predators. Whether this is an initial decision of God or a product of the evolution we do not know. Anyhow it is a fact. Our model gives the simplest dynamical description of this fact. The prey alone can only grow up to its solar saturation. The predator can only predate, and tries to increase its own number  $p(t)$ , which, after a transient, tends to the equilibrium value  $\tilde{p}$ . Moreover the predator may try to modify its coupling parameters  $\alpha$  and  $\gamma$  in order to reach the maximum equilibrium value  $\tilde{p}^{\max}$ . This process implies a loss of the prey population. The best predator is the one that gets the maximum advantage from the minimum loss of the prey, because too little prey implies decreasing predator. So the good predator tries to organize its activity in such a way that

$$\gamma \rightarrow 1,$$

and the result shown in fig. 8 indicates that *the good predator maximizes its number at the same time maximizing the global solar efficiency.*

This is the intelligent predator, the one that does not waste uselessly the prey. The good predator predate taking care of its prey.

Is this the behaviour of humankind? The answer is clearly “no”. Humankind exploits not the solar harvest, but mainly the nonrenewable resources. Humankind grows by feeding on the fossil resources. This implies a completely different model.

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